

***Marphysa belli* (Polychaeta: Eunicidae) and two related species,
Marphysa oculata and *M. tospinata*, a new species, with notes on
size-dependent features**

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Abstract.—Three morphologically related species, *Marphysa belli*, *Marphysa oculata* and *Marphysa tospinata* are described or re-described based on a morphometric study. The morphological differences among these species are discussed. The developmental patterns of antennae, branchiae and setae are emphasized.

Since the establishment of *Marphysa belli* in 1833 by Audouin and Edwards from the French side of the English Channel, this species has been widely reported from other regions of the world, such as Plymouth, England (McIntosh 1910), New England region of the U.S.A. (Pettibone 1963), and the Gulf of Mexico (Treadwell 1921, Gathof 1984). *Marphysa belli* is unique in having both compound falcigers and compound spinigers in the anterior region and in having well-developed branchiae restricted to a short anterior region. With a large number of specimens at hand, this study examines the validity of the cosmopolitan distribution of *M. belli* and the correlation between the variation of certain morphological characters and body size (width) of the specimens.

All specimens were observed with stereo and compound light microscopes. Sketches for the illustrations were made using a camera lucida. The statistical figures were produced with the program Origin. For the correlation coefficients, the confidence limits were set at 0.05.

Marphysa belli Audouin & Edwards, 1833
Figs. 1a–j, 2–6

Material examined.—Gulf of Mexico, off Florida, USNM 090007 ($n = 2$). Atlan-

tic Coast of U.S.A.: USNM 9166 ($n = 1$), USNM 28955 ($n = 1$), USNM 56988 ($n = 2$), USNM 109810 ($n = 2$), USNM 109817 ($n = 1$), USNM 109820 ($n = 4$), USNM 109823 ($n = 1$), USNM 109825 ($n = 7$), USNM 109829 ($n = 1$), USNM 109830 ($n = 2$), USNM 109831 ($n = 3$), USNM 109838 ($n = 1$), USNM 109843 ($n = 4$), USNM 109844 ($n = 3$), USNM 120624 ($n = 1$), USNM 145277 ($n = 1$), USNM 145280 ($n = 1$), USNM 145281 ($n = 1$), USNM 145282 ($n = 2$), USNM 145283 ($n = 1$), USNM 145284 ($n = 1$), USNM 145287 ($n = 1$), USNM 145290 ($n = 1$), and USNM 145294 ($n = 1$). English Channel, France, St. Malo area, Lancieux: NMW.Z.1991.067.2 ($n = 2$, Natural History Museum of Wales). English Channel, France, Bay of Seine: LA073A ($n = 10$, Natural History Museum of Paris) and LAW3A ($n = 5$, Natural History Museum of Paris). The following description is mainly based on a specimen from the Woods Hole region of Massachusetts (USNM 28955).

Abbreviations.—For the prostomial appendages, AI indicates the lateral palps, AII the paired inner lateral antennae and AIII the single median antenna. Species descriptions, including the jaw formulae, are pre-

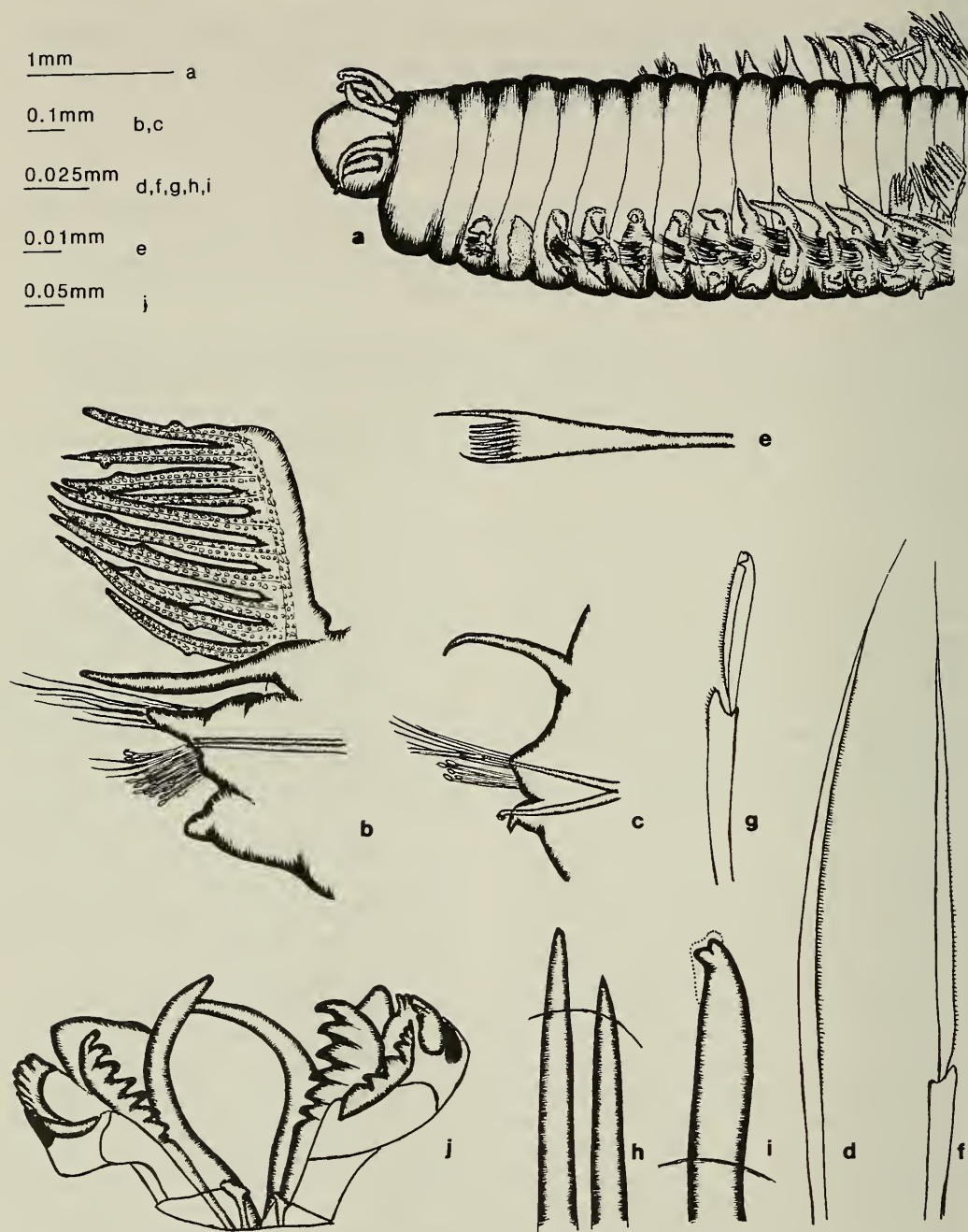


Fig. 1. *Marphysa belli*: a, anterior end, lateral view (USNM 28955); b, 14th parapodium; c, 91st parapodium; d, limbate seta; e, pectinate seta; f, compound spiniger; g, compound falciger; h, aciculae; i, subacicular hook; j, maxillae (USNM 109830).

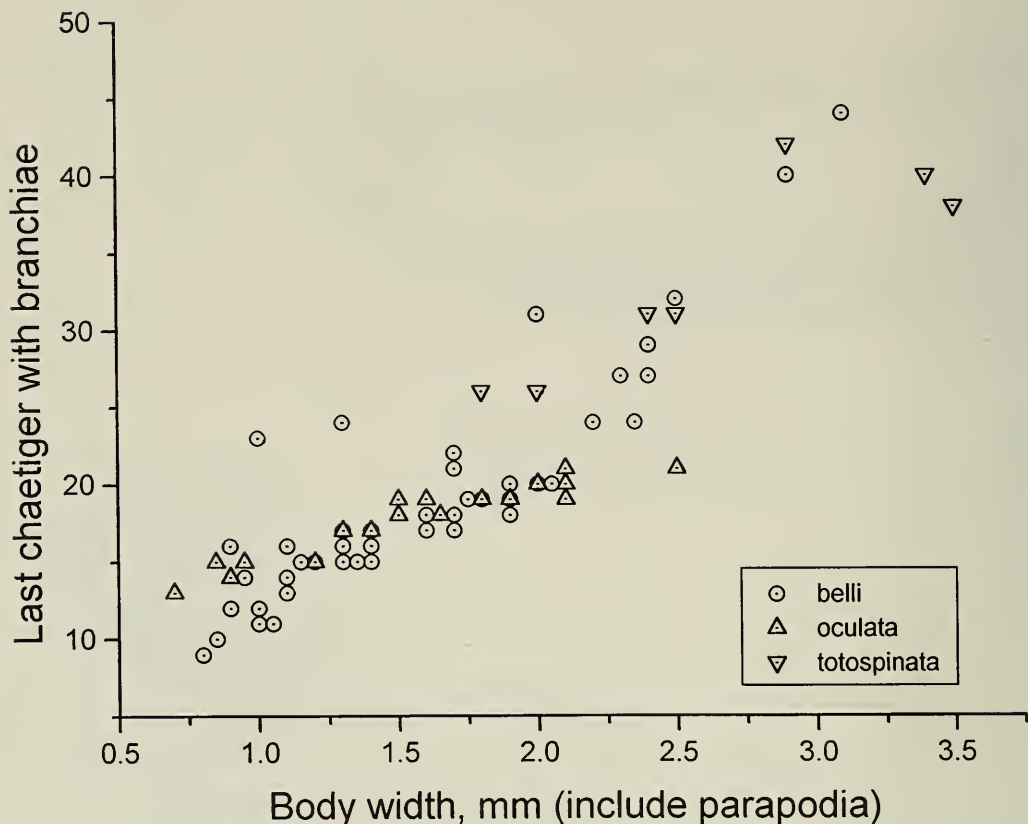


Fig. 3. Size-dependent variation of the last chaetiger with branchiae in *M. belli* ($n = 49$), *M. oculata* ($n = 18$) and *M. tospinata* ($n = 7$).

1f) present from first to about 55th parapodia, situated on posteroventral side of parapodia, with shaft and one side of blade serrated. Compound falcigers (Fig. 1g) present throughout body, arranged in about 3 rows on anteroventral side of parapodia; blade bidentate, with serrated hood and shaft; compound falcigers at least twice as numerous as compound spinigers in any chaetiger in which both kinds of setae occur. Aciculae (Fig. 1h) 2-3 in number in anterior region, becoming single from anterior-middle region; honey color, becoming darker towards posterior end; blunt-headed anteriorly, sharper in posterior region. Subacicular hook (Fig. 1i) bidentate with hood, present from 32nd parapodia, always single, except for replacement; honey to dark honey color.

Maxillary formula (Fig. 1j): 1+1, 6+6, 0+6, 8+4, 1+1 (USNM 109820); 1+1, 7+6, 0+6, 8+4, 1+1 (USNM 109830); 1+1, 8+7, 0+8, 9+4, 1+1 (USNM 109831); 1+1, 8+7, 0+7, 9+5, 1+1 (LAW3A); 1+1, 7+6, 0+6, 7+5, 1+1 (LA073A).

Remarks.—The beginning of branchiae (Fig. 2), the ending of branchiae (Fig. 3), the maximum number of branchial filaments (Fig. 4), the ending of the compound spinigers (Fig. 5) and the beginning of the subacicular hook (Fig. 6) are all size-dependent features (see Table 1). The ending of compound spinigers occurs several chaetigers posterior to the beginning of the subacicular hook.

Of 63 specimens examined, only six are complete. Four complete larval specimens, USNM 109818 (49 chaetigers, 0.8 mm

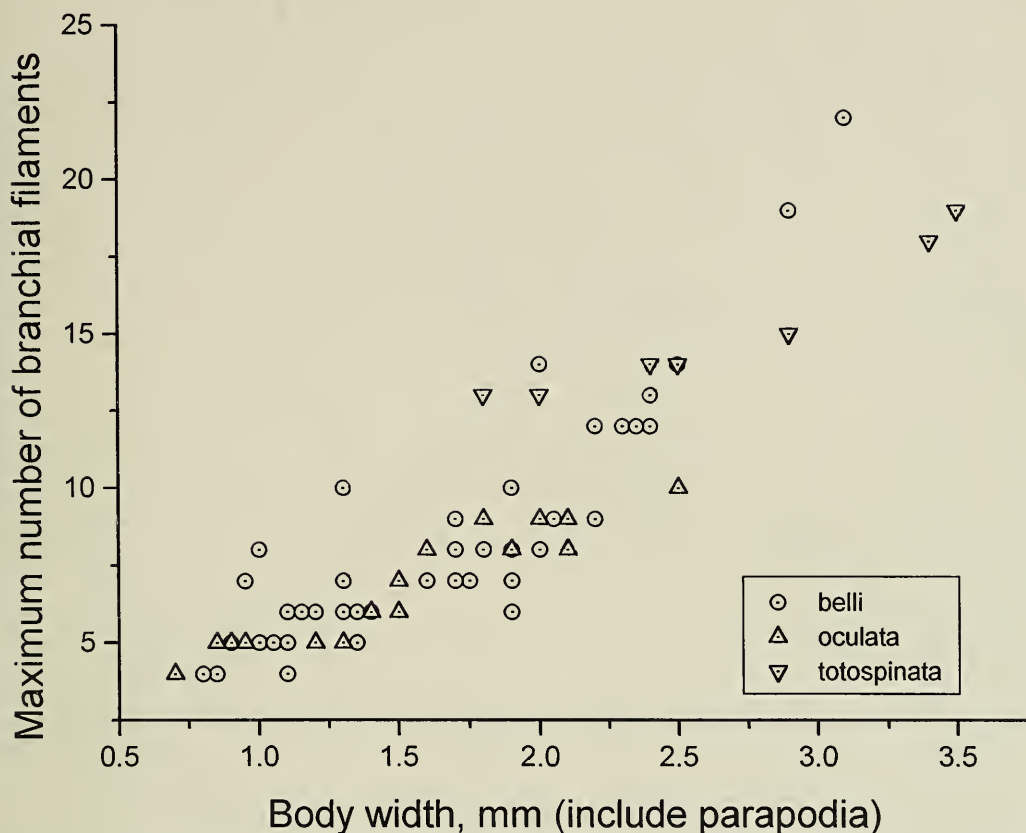


Fig. 4. Size-dependent variation of the maximum number of branchial filaments in *M. belli* ($n = 49$), *M. oculata* ($n = 17$) and *M. tospinata* ($n = 7$).

wide), USNM 109817 (70 chaetigers, 0.9 mm wide), USNM 145290 (58 chaetigers, 0.85 mm wide) and USNM 145294 (88 chaetigers, 1.05 mm wide), have only three antennae developed; the lateral palps (AI) have not appeared. Three other incomplete specimens (USNM 56988, 145280, 109820), have a body width of 0.9–1.05 mm and also have only three antennae developed. One complete specimen, USNM 109825 (77 chaetigers, 1.1 mm wide), has three antennae and two palps developed; two other small incomplete specimens, USNM 109825 (1.2 mm wide) and USNM 145277 (1.1 mm wide), also have antennae and palps. These observations suggest that *M. belli* does not develop its palps until it reaches about 80 chaetigers and a body width around 1.1 mm.

One pair of very light-colored reniform eyes was observed in most of the specimens from the Atlantic coast of the U.S.A., such as in USNM 109820. For specimens from the French coast of the English Channel, those collected two decades ago, eyes are not observed. All recently collected specimens have distinctive eyes. It is likely that the absence of eyes in preserved specimens of *M. belli* is an artifact of prolonged preservation.

When one of us (HL) visited the Natural History Museum in Paris, the type specimen of *M. belli* from the Island of Chausey was not available. However, many specimens from around the type locality, such as St. Malo, which is in the same bay as the type locality, were examined. Audouin & Edwards' (1833) original description is

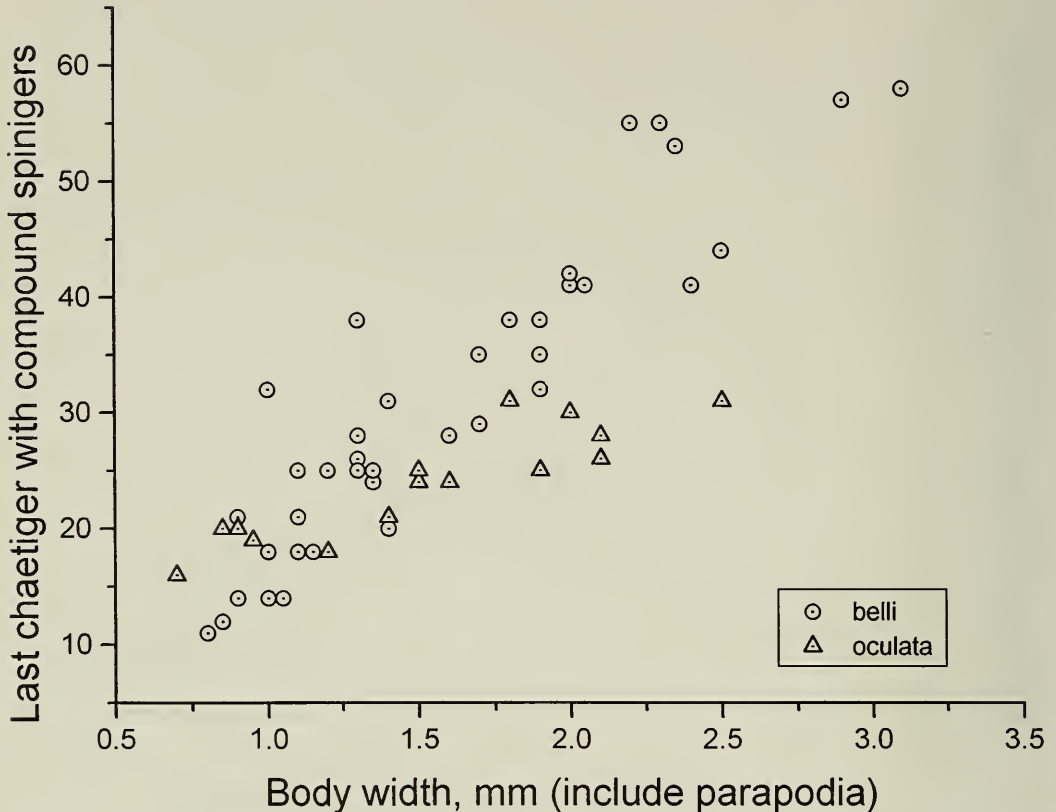


Fig. 5. Size-dependent variation of the last chaetiger with compound spinigers in *M. belli* ($n = 40$) and *M. oculata* ($n = 15$).

very simple, and it does not contradict the features we observed in these specimens.

Geographic distribution.—*M. belli* has a wide geographic distribution. It not only occurs on the French side of the English Channel but is also found along much of the Atlantic coast of the U.S.A. (Massachusetts, Delaware, Georgia) and from one station in the Gulf of Mexico, off Florida.

Marphysa oculata Treadwell, 1921
(Char. emend.)

Figs. 2–6, 7a–j, 8

Material examined.—North Atlantic Ocean, Gulf of Mexico, USA, off Florida, Dec 1982 or Jun 1983 (USNM 129779), 25°17'48"N, 81°39'48"W, SOFLA, 14 m, STA 52, $n = 12$; USNM 129706, $n = 2$; USNM 130127, $n = 1$; USNM 130256, n

$= 2$; USNM 130368, $n = 6$; USNM 130484, $n = 1$. The following description is based mostly on the catalogued specimen USNM 129779.

Description.—Specimen complete, with 120 chaetigers. First 10 chaetigers measure 2.1 mm in length, widest region (with parapodia) measures 2.2 mm. Two pairs of anal cirri; long dorsal pair reaching last 5 chaetigers; small ventral pair only $\frac{1}{3}$ length of dorsal pair.

Prostomium distally round and entire (Fig. 7a); slightly narrower than peristomium, subequal in length and less than $\frac{1}{2}$ depth of, peristomium. Three antennae (AII and AIII) and two palps (AI), irregularly slightly wrinkled, evenly spaced, short, similar in thickness. Length of AI:AII:AIII = 1:1.3:1.4. AII and AIII extending to near

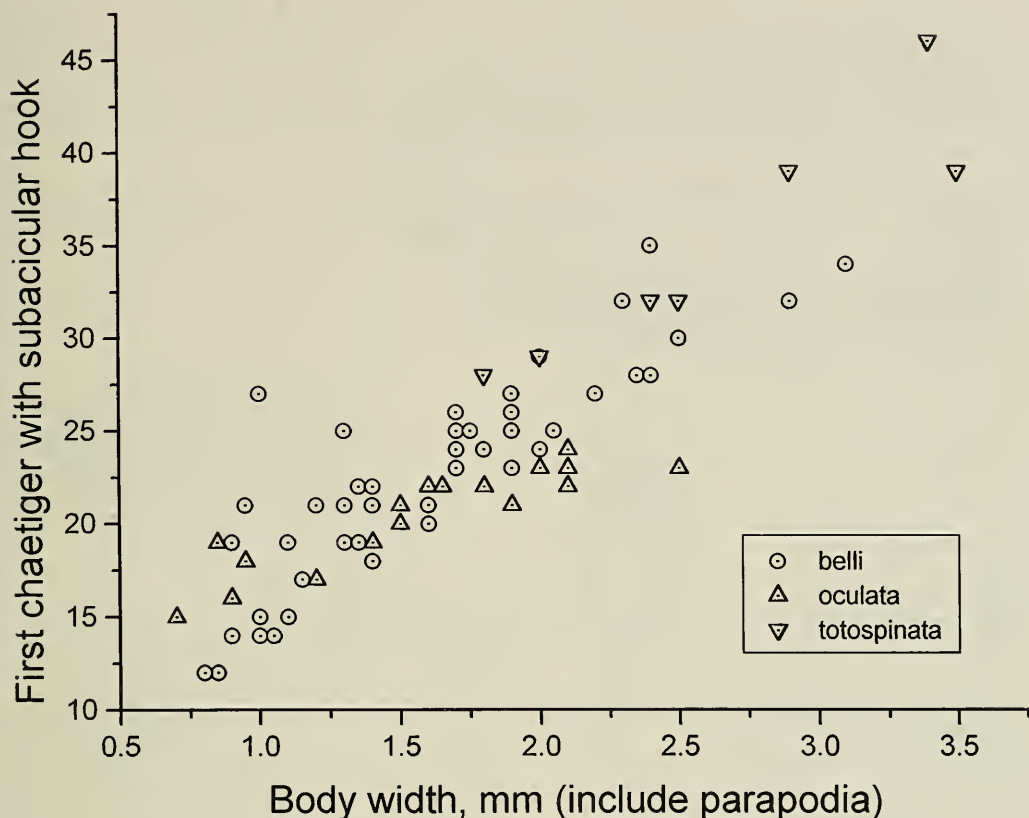


Fig. 6. Size-dependent variation of the first chaetiger with subacicular hook in *M. belli* ($n = 49$), *M. oculata* ($n = 17$) and *M. tospinata* ($n = 7$).

anterior end of prostomium. One pair of large, black oval eyes outside of AII and posterior to AI, partly covered by peristomium. First ring of peristomium $\frac{2}{3}$ (dorsally) to $\frac{3}{4}$ (ventrally) of total peristomial length. No peristomial cirri.

First chaetiger equal in length to second ring of peristomium, following chaetigers broader and longer. First parapodia smaller than others. Dorsal cirri long throughout body, always longer than ventral cirri. Postsetal lobe long in anterior parapodia (Fig. 7b), absent from chaetigers with subacicular hook. Ventral cirri digitiform throughout body, becoming smaller from about first chaetiger lacking prominent postsetal lobe.

Pectinate branchiae present from 10th to 19th parapodia, with 9 filaments, individual filaments slightly longer than dorsal cirri. Limbate setae (Fig. 7c) longest, finely ser-

rated on one edge. Pectinate setae (Fig. 7d) present in anterior body region, with 7–11 teeth, tooth on one edge longer, more stout than others, tooth on other edge slightly longer than others. Compound falcigers bidentate (Fig. 7e, f), present from 16th parapodia, shaft and base of hood serrated. Compound spinigers (Fig. 7g) serrated on blade and shaft, present on first to 27th parapodia, 20 or more compound spinigers on 10th parapodia. Aciculum (Fig. 7h) with blunt head; yellow to very light honey in color; up to 3 aciculae present from 6th to 8th parapodia, only 1 aciculum present from 14th parapodia to posterior end. Subacicular hook (Fig. 7i) bidentate, with hood, distal tooth small and directed obliquely, proximal tooth directed laterally; yellow to very light honey in color; present from 23rd parapodia, always single, except for replacement.

Table 1.—Correlations between body width (X, mm) and the morphometric characters (Y), which is expressed by linear regression “ $Y = AX + B$,” in *Marphysa belli* ($n = 49$), *M. oculata* ($n = 17$) and *M. tospinata* ($n = 7$). *SD* is standard deviation. *R* is coefficient. The morphometric characters are: the first chaetiger with branchiae (FB), the last chaetiger with branchiae (LB), the maximum number of branchial filaments (MB), the first chaetiger with subacicular hook (SH), the last chaetiger with compound spiniger (CS) and the first chaetiger with compound falciger (CF).

| Y | A \pm SD | B \pm SD | R |
|------------------------|------------------|------------------|------|
| <i>M. belli</i> FB | 5.30 \pm 0.51 | 3.27 \pm 0.30 | 0.85 |
| <i>M. belli</i> LB | 1.15 \pm 1.56 | 11.23 \pm 0.92 | 0.87 |
| <i>M. belli</i> MB | -1.30 \pm 0.81 | 5.81 \pm 0.48 | 0.87 |
| <i>M. belli</i> SH | 8.46 \pm 1.22 | 8.80 \pm 0.72 | 0.87 |
| <i>M. belli</i> CS | -1.55 \pm 2.43 | 20.60 \pm 1.43 | 0.92 |
| <i>M. oculata</i> FB | 7.18 \pm 0.39 | 1.17 \pm 0.24 | 0.78 |
| <i>M. oculata</i> LB | 10.70 \pm 0.62 | 4.50 \pm 0.38 | 0.95 |
| <i>M. oculata</i> MB | 1.57 \pm 0.50 | 3.46 \pm 0.31 | 0.95 |
| <i>M. oculata</i> SH | 13.16 \pm 0.96 | 4.61 \pm 0.58 | 0.90 |
| <i>M. oculata</i> CS | 11.56 \pm 1.75 | 8.03 \pm 1.08 | 0.90 |
| <i>M. oculata</i> CF | -5.40 \pm 1.96 | 10.96 \pm 1.21 | 0.93 |
| <i>M. tospinata</i> FB | 11.90 \pm 0.63 | 0.63 \pm 0.23 | 0.78 |
| <i>M. tospinata</i> LB | 9.77 \pm 5.51 | 8.95 \pm 2.03 | 0.89 |
| <i>M. tospinata</i> MB | 5.85 \pm 1.31 | 3.51 \pm 0.48 | 0.96 |
| <i>M. tospinata</i> SH | 10.70 \pm 4.66 | 9.20 \pm 1.72 | 0.92 |

Maxillary formula (Fig. 7j): 1+1, 6+5, 0+5, 7+4, 1+1 (USNM 129779); 1+1, 6+5, 0+5, 9+3, 1+1 and 1+1, 7+6, 0+6, 6+4, 1+1 (USNM 130368).

Remarks.—According to morphometric data, the size-dependent morphological variation is distinctive in this species.

Antennae: we have a complete specimen with 71 chaetigers which possesses three antennae but lacks the lateral pair of palps (AI), whereas several other specimens with about 84 chaetigers possess the lateral palps. These observations suggest that the palps of *M. oculata* do not develop until it reaches about the 80-chaetiger stage. This estimation is comparable to the palp developmental pattern of *Marphysa belli*. The palp development of these two species of *Marphysa* is much later when compared to that of *Eunice wui* (Lu & Fauchald 1998), whose palps emerge after the worm reaches about 30 chaetigers in size. However, both *Eunice* and *Marphysa* of the Eunicidae develop their lateral palps much later than species in the Onuphidae. For example, *Notonuphis antarctica* (our observations), *Nothria elegans* (Blake 1975), *Mooreonu-*

phis jonesi (Fauchald 1982) and *Kinbergonuphis simoni* (Hsieh & Simon 1987) have developed the lateral palps when they are only 5 chaetigers in size. It appears that the pattern of development of the palps is more uniform among the Onuphidae when compared to the Eunicidae.

Branchiae: before the development of the palps, the branchiae are already well developed. During the development of the worm, the starting chaetiger with branchiae changes from the 8th parapodia to the 10th parapodia (Fig. 2, Table 1); the ending chaetiger with branchiae changes from the 13th parapodia to the 21st parapodia (Fig. 3, Table 1); the number of branchiae changes from only 6 pairs to 12 pairs; the maximum number of branchial filaments changes from 4 to 10 (Fig. 4, Table 1).

Compound falcigers (Fig. 8, Table 1): their number is always less than that of the compound spinigers in any given segment in which both occur. In young worms (0.7 mm wide), compound falcigers are present in all chaetigers. When the worm grows, compound falcigers are lost from a certain number of anterior chaetigers. The loss



Fig. 7. *Marphysa oculata*: a, anterior end, lateral view (USNM 129779); b, 15th parapodium; c, limbate seta; d, pectinate seta; e, f, compound falcigers; g, compound spiniger; h, aciculum; i, subacicular hook; j, maxillae.

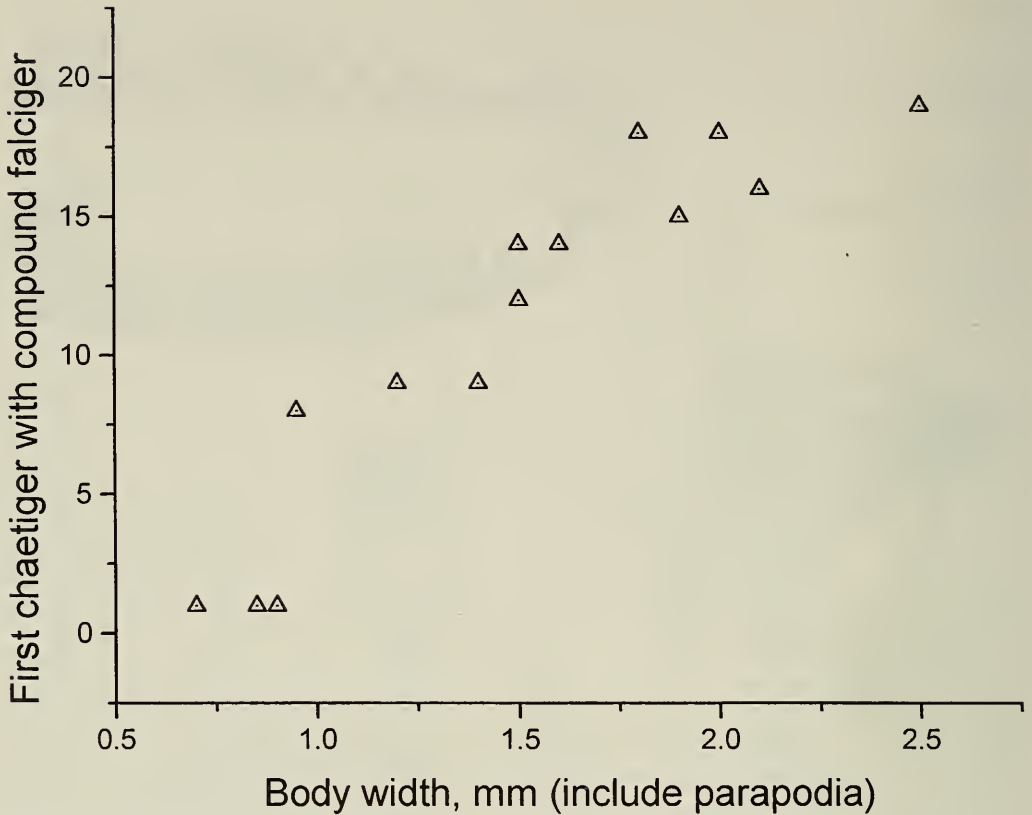


Fig. 8. Size-dependent variation of the first chaetiger with compound falcigers in *M. oculata* ($n = 15$).

starts at about chaetiger 8 and proceeds from there in both directions. For a 2.5 mm wide worm, compound falcigers are absent in the first 19 parapodia.

Compound spinigers (Fig. 5, Table 1): the ending position of the compound spinigers is size-dependent and varies from the 16th chaetiger to the 31st chaetiger.

Subacicular hook (Fig. 6, Table 1): the first occurrence of a subacicular hook changes from the 15th parapodia to the 24th parapodia. It always occurs several chaetigers after the ending of the branchiae and several chaetigers before the ending of the compound spinigers.

The sensory organ reported by Hayashi & Yamane (1994) for *Marphysa sanguinea* is also observed on the ventral base of dorsal cirri (22rd parapodia) of *M. oculata* (USNM 130127).

Treadwell (1921) described a single incomplete specimen from Key West Harbor, Florida (close to our collection site) as *Marphysa belli*, variety *oculata* based on the presence of eyes in his specimen versus the absence of eyes in European specimens, though he mentioned with contradiction that "Since the presence or absence of eyes does not in itself seem to me of specific importance, I have regarded this as merely a varietal difference." As indicated earlier, the eye condition of *M. belli* is likely related to preservation. Treadwell's description on *M. belli*, variety *oculata* totally agrees with our specimens, especially for the setal distribution, i.e., compound spinigers are the main compound setae in the anterior region. Thus, we believe that they belong to the same species. Unfortunately, Treadwell (1921) did not mention the consistent dif-

ferences between his species and *M. belli*. In the anterior body region, there are at least twice as many compound falcigers than compound spinigers in *M. belli*, whereas in *M. oculata* the compound spinigers are at least twice as common as the compound falcigers, or the compound falcigers may be absent in some anterior parapodia. Only after the observation of many specimens (*M. oculata*, $n = 24$; *M. belli*, $n = 63$) did this morphological difference between the two species become obvious, thereby warranting a separate species status for *M. oculata*.

Marphysa tospinata, new species

Figs. 2–4, 6, 9a–h

Material examined.—Atlantic coast, Ireland, Mayo, near Blacksod Bay (Holotype: NMW.Z.1988.069.84, and 6 paratypes: NMW.Z.1988.069.84 and NMW.Z.1988.069.84).

Description.—Specimen complete, with 322 chaetigers. Two pairs of anal cirri; longer dorsal pair reaching last 4 chaetigers. First 10 chaetigers measure 3.4 mm in length, widest region measures 5.9 mm.

Prostomium distally round and entire (Fig. 9a), slightly narrower than, same length and $\frac{1}{2}$ depth of, peristomium. Three antennae (AII and AIII) and two palps (AI), slightly irregularly wrinkled, same size, evenly spaced; length of AI:AII:AIII = 1:1.2:1.4; all extend past anterior end of prostomium, AI reaching first ring of peristomium, AII reaching second ring of peristomium, AIII reaching anterior end of first chaetiger. One pair of light brown reniform eyes between AI and AII. First ring of peristomium about $\frac{2}{3}$ of total length (dorsal view). No peristomial cirri.

Anterior four chaetigers thick and cube-shaped; becoming flatter dorsoventrally from fifth chaetiger. First parapodia smaller than others. Dorsal cirri long, finger-shaped from beginning, becoming slender in posterior region; dorsal cirri always longer than ventral cirri. Ventral cirri with oval base in

anterior chaetigers, becoming slender posteriorly. Postsetal lobe long in anterior parapodia until about 65th parapodia, length comparable to dorsal and ventral cirri in some chaetigers. Sensory organ similar to that described by Hayashi & Yamane (1994) for *Marphysa sanguinea* and *M. oculata* also observed on ventral base of dorsal cirri of 286th parapodia (Fig. 9b).

Pectinate branchiae present from 14th–40th parapodia. Twelveth parapodia with 11 filaments, as many as 18 filaments observed on 27th parapodia. Individual branchial filaments slightly longer than dorsal cirri. Branchiae completely cover dorsal region of worm.

Serrated limbate setae longest of those situated on dorsal side of parapodia. Pectinate setae (Fig. 9c) present from anterior parapodia; with 8–9 teeth, tooth on one edge longer, more stout than others, tooth on other edge slightly longer than others. Compound falcigers (Fig. 9d) present throughout body, with serrated hood and serrated shaft; more than 20 compound falcigers arranged in several rows on anteroventral side of parapodia, fewer in number on posterior side. Compound spinigers (Fig. 9e) present from beginning till very posterior end, such as on parapodium 286 (Fig. 9b); serrated on shaft and one side of blade; 6–7 compound spinigers arranged in a line on posteroventral side of parapodia, decreasing to 1–2 in number in posterior region. Compound falcigers at least twice as numerous as compound spinigers in anterior parapodia. Aciculae (Fig. 9f) 3–4 in anterior region, single or occasionally double from middle-anterior region; honey color, becoming darker in posterior region; blunt-headed, with sheath. Subacicular hook (Fig. 9g) from 46th parapodia, single in 75% of parapodia, double in those remaining; honey to dark honey color; bidentate with hood.

Maxillary formula (Fig. 9h): 1+1, 7+6, 0+7, 8+5, 1+1 in one paratype (NMW.Z.1988.069.86).

Remarks.—The beginning (Fig. 2) and

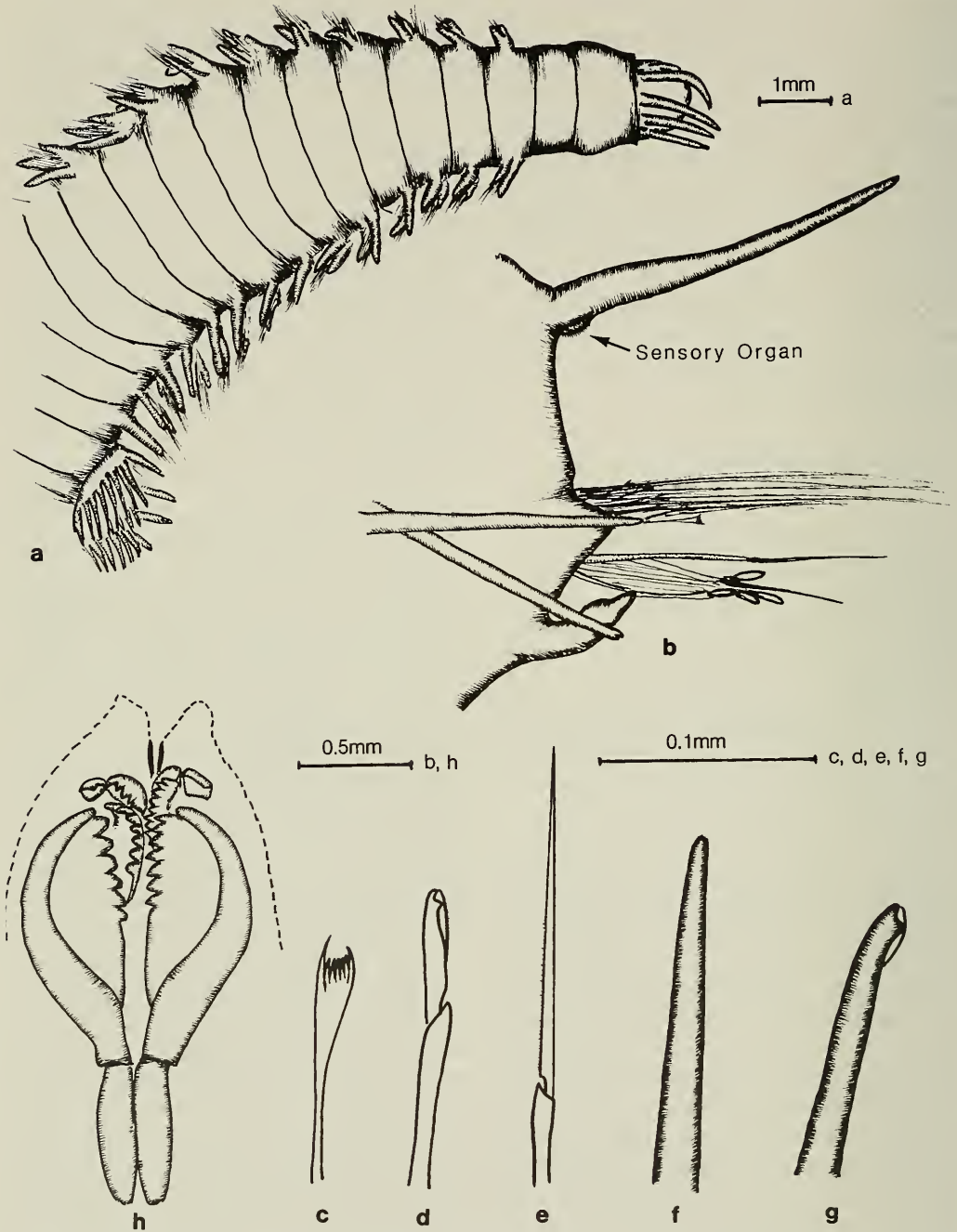


Fig. 9. *Marphysa totespinata*, new species: a, anterior end, dorsal view (NMW.Z.1988.069.84); b, 286th parapodium; c, pectinate seta; d, compound falciger; e, compound spiniger; f, aciculum; g, subacicular hook; h, maxillae (NMW.Z.1988.069.86).

ending (Fig. 3) position of branchiae, the maximum number of branchial filaments (Fig. 4) and the starting position of the subacicular hook (Fig. 6) of *M. tospinata* are all size-dependent characters (see Table 1). This species ($n = 7$) is consistently different from *M. belli* ($n = 63$) and *M. oculata* ($n = 24$) in its setal arrangement: in the anterior parapodia, compound spinigers are the dominant setal type in *M. oculata*, whereas in *M. tospinata* compound falcigers are more numerous; in *M. belli*, compound spinigers occur on less than $\frac{3}{4}$ of the anterior parapodia, whereas in *M. tospinata* compound spinigers are present nearly throughout the entire body.

McIntosh (1910) described a specimen of *M. belli* from the Plymouth region. According to his description, compound spinigers exist from the beginning to the posterior end of the worm. If this is the case, his specimen should belong to *M. tospinata*.

Etymology.—The species is named for its special morphological character, which is the occurrence of compound spinigers throughout the body length.

Discussion

The branchial and setal patterns are size-dependent morphological characters in *Marphysa belli* and its two related species, *M. oculata* and *M. tospinata*. Among the 15 sets of correlations calculated at a confidence limit of 0.05 (Table 1), the range of coefficients (R) is between 0.78 and 0.96 (average = 0.89). The general morphological variations fall in a similar range between *M. belli* and *M. oculata* and between *M. belli* and *M. tospinata*, for a similarly sized specimen. Slight morphometric differences exist between *M. oculata* and *M. tospinata*. For example, in a specimen of *M. oculata* that is 2.5 mm wide, its branchiae begin on the 10th parapodia and end on the 22nd parapodia, and its subacicular hook emerges from the 23rd parapodia, whereas for a similarly sized specimen of *M. tospinata*, its branchiae begin on the

13th parapodia and end on the 32nd parapodia, and its subacicular hook emerges from the 32nd parapodia. Though only relatively small sized specimens of *M. oculata* and large sized specimens of *M. tospinata* were available for the present study, several specimens of both species have overlapping size ranges. In addition, both species show distinctive features when compared to similarly sized specimens of *M. belli*, whose size ranged from small (larva) to large specimens. These observations support the suggestion that *M. oculata* is not the juvenile stage of *M. tospinata*. The arrangement of compound setae is the major difference among these species. If additional specimens of *M. belli* from other areas of the world, such as the Mediterranean, South Africa and Indochina, can be examined, it is possible that new sister species can be separated. This species group potentially provides a good case for further biogeographic study.

Key to the *Marphysa belli* group

- 1. At least twice as many compound falcigers than compound spinigers in anterior parapodia 2
- 1'. At least twice as many compound spinigers than compound falcigers in anterior parapodia *M. oculata*
- 2. Compound spinigers limited to anterior $\frac{1}{3}$ body region or less *M. belli*
- 2'. Compound spinigers present along nearly the entire body *M. tospinata*

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